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Taxonomic Characters in the Genus *Echinococcus* (Cestoda: Taenlidae)

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Taxonomic Characters in the Genus *Echinococcus* (Cestoda: Taeniidae)

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Not more than 4 species of cestodes of the genus Echinococcus *Rudolphi, 1801, are recognised as valid. The larval stage of at least 3 of them is able to develop in man, causing respective types of hydatid disease. Accurate characterization of these cestodes, including both larval and adult stages, is essential for identification, upon which depends development of methods for preventing infection of man and domestic animals. Because morphological characteristics of the larval cestodes may be modified according to the species of host in which they develop, identification should be based upon taxonomic characters of specimens from the respective natural hosts, which can be identified by means of ecological investigations in endemic areas in combination with controlled infection of experimental animals. The morphological and biological characteristics of the known species are discussed, and the two species most important to public health and economically—*E. granulosus *(Batsch, 1786) and* E. multilocularis *Leuckart, 1863—are distinguished.*

Recent revisions of the genus *Echinococcus* Rudolphi, 1801, place within it not more than 4 species: *E. granulosus* (Batsch, 1786); *E. multilocularis* Leuckart, 1863; *E. oligarthrus* (Diesing, 1863); and *E. patagonicus* Szidat, 1960 (Rausch & Nelson, 1963; Verster, 1965). The specific distinction of *E. oligarthrus* has been confirmed recently by Thatcher & Sousa (1966). The status of *E. patagonicus*, known only from the strobilar stage, is still uncertain.

In characterizing these cestodes, it is important to define taxonomic characters on the basis of natural parasite–host relationships. Undue emphasis on relationships existing under conditions modified by man tends to obscure differences that otherwise may be well expressed. Misconceptions have arisen also from the tendency to exaggerate the significance of the atypical or the aberrant, particularly in connexion with the larval cestodes in other than their natural hosts.

This paper attempts to define the morphological and biological characteristics which serve to distinguish *E. granulosus* and *E. multilocularis*; *E. oligarthrus* and *E. patagonicus* are considered only briefly. Unless otherwise indicated, the following material has been taken largely from Rausch (1967a).

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CHARACTERISTICS OF *ECHINOCOCCUS* SPECIES

Species of *Echinococcus* are adapted to hosts having a well-defined predator-prey relationship. At higher latitudes, where *E. granulosus* exists under natural conditions, the final host is the wolf, *Canis lupus* L., and the larval cestode occurs in various species of wild ruminants upon which wolves regularly prey. Wild herbivores of species that became domesticated (e.g., wild swine, aurochs, etc.) were no doubt also involved in the life-cycle of *E. granulosus*. Through the domestication of various animals, a synanthropic cycle became established, domestic ungulates replacing their wild progenitors and the domestic dog replacing the wolf. As a result of introductions of domestic animals from Europe to other parts of the world, *E. granulosus* has become almost cosmopolitan in distribution. Introduction of this cestode into new ecosystems has occasionally resulted in the involvement in its life-cycle of mammals quite disparate phylogenetically from its natural hosts (e.g., certain marsupials in Australia).

The adult *E. granulosus* is not strictly host-specific, for it has been recorded from a variety of wild carnivores (Nelson & Rausch, 1963; Smyth & Smyth, 1964; Verster, 1965). This tapeworm is sometimes found in species of mammals which are not suitable hosts; in such cases, strobilar development is abnormal and eggs usually are not produced. The

presence of very small numbers of cestodes in a given carnivore is often indicative of unsatisfactory parasite–host relationships.

The larvae of *E. granulosus*, adapted to development in a comparatively long-lived intermediate host, grow relatively slowly. Only after a period of years is maximum productivity of protoscolices attained; in older individuals of the natural hosts, therefore, large cysts containing great numbers of protoscolices are found. The larval *E. granulosus* has been recorded in a wide variety of wild and domestic herbivores, and larvae have been reported occasionally even from carnivores.

E. multilocularis appears to be limited distributionally to the northern hemisphere, where the adult cestode occurs naturally in foxes of the genera *Vulpes* and *Alopex*. Naturally infected wolves have been found in the Soviet Union (Petrov & Čertkova, 1959; Kadenatsii, 1959, cited by Petrov & Delianova, 1962). Cestodes in domestic cats usually produce eggs (Vogel, 1957; Petrov & Lukašenko, 1962; Rausch, unpublished data). In general, the strobilar stage of *E. multilocularis* appears to be much more host-specific than is that of *E. granulosus*. The domestic dog may be the final host for both species, and both can develop synchronously in a single dog (Rausch, unpublished experimental data); presumably this could occur under natural conditions in the wolf.

Microtine rodents and other small mammalian prey of foxes serve as the intermediate host of *E. multilocularis*. Mammals of the following genera have been found naturally infected: *Sorex*, *Ochotona*, *Sciurus*, *Citellus*, *Apodemus*, *Peromyscus*, *Lemmus*, *Ondatra*, *Ellobius*, *Allactaga*, *Rhombomys*, *Meriones* —1 species each; *Clethrionomys*—3 species; *Microtus*—5 species. Small mammals of various additional species, mainly rodents, have been shown experimentally to be capable of serving as the intermediate host of this larval cestode. *E. granulosus* and *E. multilocularis* are not known to share any intermediate host, although a few mammals have been found to be susceptible to infection by the larvae of both (e.g., man).

Those rodents that serve as the intermediate host of *E. multilocularis* are animals with a short life-span, usually not more than a year. Adapted to such hosts, the larval *E. multilocularis* develops rapidly, reaching maximum productivity of protoscolices within a few months. Larvae only 60–70 days old contain some infective protoscolices (Rausch & Fay, unpublished data).

E. oligarthrus appears to be restricted distributionally to Central and South America. It is known only from wild felids, and as suggested by Cameron (1926), the larval cestode described as *E. cruzi* Brumpt & Joyeux, from a large rodent, *Dasyprocta agouti* Erxleben, may represent the larval stage. Some evidence exists to indicate that the larval *E. oligarthrus* can develop in man (Thatcher & Sousa, 1966). *E. patagonicus* is evidently known only from wild canids of the genus *Dusicyon*, in Patagonia. The natural intermediate host is not known. Szidat (1963) suggested that the larva may produce in man an alveolar formation similar to that caused by *E. multilocularis*.

MORPHOLOGICAL CHARACTERISTICS

The taxonomic value of morphological characters in species of *Echinococcus* (strobilar stage) has been discussed by Rausch (1953), Vogel (1957), Verster (1965), and others. The size of the strobila, position of the genital pore, number and distribution of testes and form of the gravid uterus are taxonomically important at the specific level (Rausch & Schiller, 1954; Vogel, 1957; Petrov & Čertkova, 1959).

Size, shape and number of rostellar hooks, dimensions of the cirrus sac in mature segments and size of embryophore ought to be considered in attempting to identify species of *Echinococcus*, even though these characters have been found to be of limited taxonomic value. The rostellar hooks vary widely in number and, in even a single strobila, in size and shape. Since the size of the rostellar hooks is related to age of the strobila, useful comparisons can be made in cestodes of known age from experimentally infected animals.

A total of 9 subspecies of *E. granulosus* has been distinguished, largely on the basis of morphological characteristics. Of these subspecies, 8 are neither allopatric nor ecologically segregated; thus, the defined differences appear to represent only non-significant morphological variation (Rausch, 1967b).

In the larval stage, neither *E. granulosus* nor *E. multilocularis* is host-specific in a strict sense. Besides the natural intermediate hosts, which provide optimum conditions for development of the respective larval cestodes, mammals representing a variety of species support some degree of development. In some of the least suitable, the larvae seem barely to survive; here, proliferation of tissue takes place, but protoscolices are rarely or never formed (e.g., *E. multilocularis* in man; *E. granulosus* in the liver of cattle). In comparatively unsuitable intermediate

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hosts, development of the larval cestodes is often anomalous.

In the natural intermediate host, the larval *E. granulosus* consists of a subspherical, fluid-filled vesicle having a laminated outer layer and an inner germinal membrane. The latter gives rise to brood capsules in which protoscolices are produced. Abnormally formed larvae are sometimes found even in natural hosts (e.g., when infections are massive), and various morphological types occur in domestic animals, depending upon the species. One of the most interesting is the multicystic larva of *E. granulosus* characteristically found in the liver of cattle.

The larval *E. multilocularis* in the natural intermediate host (e.g., northern red-backed vole, *Clethrionomys rutilus* Pallas) consists of a subspherical, regular mass of vesicles arising from a single embryo. The vesicles are arranged from the centre in a somewhat radial pattern, becoming larger peripherally. Each becomes filled by small, irregularly shaped brood capsules, equivalent to those of E. *granulosus*, in which protoscolices are produced. The vesicles contain a semifluid, gelatinous material which differs in quantity in larvae from different hosts. Smyth & Smyth (1964, p. 494) stated that such material is the product of degenerative change; however, this is true only in the case of larvae developing in an atypical host (e.g., in the human liver). Some intrinsic mechanism, evidently related to the production of protoscolices, controls the extent of exogenous budding of vesicles; in red-backed voles, for example, the entire mass when fully matured and filled to capacity with protoscolices attains an average diameter of about 10 mm. In other species (e.g., muskrat, *Ondatra zibethica* L.) the aggregation of vesicles arising from a single embryo becomes larger. In heavily infected animals, the individual masses may coalesce, while in experimentally infected rodents that have received large numbers of embryophores almost the entire liver may be replaced by the larval cestodes.

Among microtine rodents of species commonly found infected in nature, characteristics of the larval *E. multilocularis* may differ from species to species (Rausch & Fay, unpublished data). In mammals other than microtine rodents, differences in pattern of development and in final form of the larva may be comparatively extreme. The invasive, necrotizing process that usually takes place in the human liver seems to represent the ultimate in parasite–host incompatibility with continued survival of both. Some morphological and biological characteristics of *E. granulosus* and *E. multilocularis* are compared in the accompanying table.

A COMPARISON OF MORPHOLOGICAL AND BIOLOGICAL CHARACTERISTICS OF *E. GRANULOSUS* AND *E. MULTILOCULARIS*

Characteristic	*E. granulosus*	*E. multilocularis*
Adult cestode:		
Hosts	Typically dog and wolf	Typically in foxes; also in dog
Size of strobila (mm)	2–6	1.2–3.7
Number of testes	45–65	17–26
Distribution of testes	Anterior and posterior to genital pore	From level of genital pore to posterior end of segment
Position of genital pore in gravid segment	Near posterior end of segment	Near middle of segment
Form of uterus	With lateral branches	Sac-like, lacking lateral branches
Larval cestode:		
Hosts	Typically ungulates	Typically rodents
Form	Usually a fluid-filled cyst	Alveolar, comprised of many small, interconnected cysts
Rate of development	Slowly developing, adapted to long-lived intermediate hosts. Protoscolices produced after 1–2 years	Rapidly developing, adapted to short-lived intermediate hosts. Infective protoscolices present in 2–3 mon hs

DISCUSSION

Characterization of a given species of *Echinococcus* is a comparatively complex undertaking, involving not only a description of the morphological features of the strobilar and larval stages, but also an evaluation of ecological and physiological factors.

Further, to make full use of valid taxonomic criteria, the definition of natural parasite–host relationships is necessary. Having accomplished this, limits of host specificity can be discerned and normally developed stages of the cestode can be recognized. The comparisons of the adult cestodes ideally should be based upon specimens of known age obtained experimentally in the natural host, and treated in a uniform manner both before and after preservation. The extent of host-related variation in the larval cestode can be determined through experimental infection of animals. Differences in rates of development and other adaptations to the respective hosts are as significant as morphological criteria in characterizing cestodes of the genus *Echinococcus*.

RÉSUMÉ

Trois espèces de cestodes du genre *Echinococcus* Rudolphi, 1801 ont été identifiées: *E. granulosus* (Batsch, 1786); *E. multilocularis* Leuckart, 1863; et *E. oligarthrus* (Diesing, 1863). On n'a pas encore déterminé avec certitude s'il fallait leur adjoindre *E. patagonicus* Szidat, 1960. Ce dernier mis à part, tous ces ténias sont connus pour provoquer chez l'homme des formes spécifiques d'échinococcose hydatique; l'infestation par les larves de *E. granulosus* est également fréquente chez les ongulés domestiques et la répartition de ce cestode est presque cosmopolite. *E. multilocularis* est très largement répandu dans l'hémisphère nord, tandis que *E. oligarthrus* ne se trouve que dans le centre et le sud de l'Amérique.

Pour définir des critères morphologiques qui permettent de distinguer avec précision les différentes espèces d'*Echinococcus*, il convient de prendre les spécimens sur leurs hôtes naturels, sinon l'évolution du stade strobilaire se trouve habituellement retardée et le stade larvaire présente une gamme étendue de variations morphologiques. Pour identifier les hôtes naturels, il faut étudier l'écologie dans les zones d'endémicité, ainsi que les manifestations de l'infection contrôlée chez des animaux d'expérience. Le stade strobilaire des ténias peut présenter plusieurs caractères spécifiques importants qui concernent notamment la taille, le nombre et la répartition des testicules, la position du pore génital dans les segments gravides, la forme de l'utérus gravide et, dans certains cas, la taille et la forme des crochets du rostre. La structure de la larve normalement développée est caractéristique de chacune des trois espèces relativement bien connues. Les caractéristiques biologiques jouent également un rôle important dans la différenciation de ces cestodes. Au stade larvaire, le laps de temps nécessaire au développement des scolex infectants est directement fonction de la durée de vie de l'hôte intermédiaire. La larve de *E. multilocularis* présente des scolex infectants dès le deuxième ou le troisième mois, alors qu'ils n'apparaissent qu'au bout d'un ou deux ans chez la larve de *E. granulosus*. Un tableau donne la liste comparative des caractéristiques taxonomiques qui permettent de faire la distinction entre ces deux espèces.

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